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A STUDY OF FACTORS IN THE DEVELOPMENT OF IPS OUTBREAKS

Progress Report of Sierra Studies - 1946

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A STUDY OF FACTORS IN THE DEVELOPMENT OF IPS OUTBREAKS

Progress Report of Sierra Studies - 1946

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INTRODUCTION

The ponderosa pine engraver, Ips confusus Lec., long known as a slash breeding bark beetle, periodic top-killer, and often considered a forerunner of western pine beetle, Dendroctonus brevicomis Lec. outbreaks, has within recent years put in a bid for a primary position among bark beetles. Its behavior in numerous sporadic outbreaks within the California pine region since 1943 has indicated in many cases a direct association with slash breeding, even where such slash had been laid down continuously throughout the season. This is in apparent contradiction to the belief by entomologists as recorded by U. S. D. A. circular 411 1/ that slash laid down continuously tended to absorb attacking populations reared in slash, and was therefore not a serious hazard.

The apparent discrepancies and inconsistencies in the behavior of Ips in these infestations, indicated a strong need for further information on habits and conditions of breeding before Ips could be controlled intelligently. In summarizing the results of Ips studies and notes of many investigators from 1913 to 1942, Miller 2/ concluded: "The accumulated information on Ips confusus gives a fairly complete picture of the distribution of this beetle and hosts in which it occurs in the California region. However, there are many gaps yet to be filled before we have a satisfactory understanding of its habits, of the factors causing its sporadic outbreaks and the basis for a sound control policy."

Continuing economic loss to commercially valuable timber, poles, and reproduction, particularly along the west front of the Sierras in the vicinity of rapidly increasing logging activity further emphasized the necessity of obtaining more basic information. Consequently, in 1945 preliminary studies were initiated in both the northern part of the state, at the Hat Creek field laboratory, and in the southern Sierra

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1/ Div. of Forest Insect Inves. 1927. The Relation of Insects to Slash Disposal. U.S.D.A. Circular 411. Washington, D.C. Sept.

2/ Miller, J.M., 1945, Summary of Information on Ips confusus. Mss. Berkeley.

sub-region, at the Miami field laboratory. The Hat Creek studies by R. C. Hall laid particular stress on the possible importance of climatic and environmental factors in the development of Ips outbreaks, while studies at the Miami field laboratory by G. R. Struble laid emphasis on the possible importance of biological and host factors.

The limited period during 1945 for study in the Miami area allowed only an appraisal of breeding in current logging slash in relation to subsequent infestations in reserve stands. A progress report 3/ in 1945 of this study in 4 major slash areas, all of which remained free from subsequent attacks in living trees, added further evidence in agreement with previous findings that a continuous slash supply absorbs Ips populations. This evidence, however, was partially refuted by heavy localized outbreaks in one of these areas late in 1946.

Investigative studies on this problem were resumed in 1946 at the Miami field base from June 15 to September 15. The primary objective sought was to determine what basic factors are responsible for sudden fluctuations in populations. In these studies an attempt was made to determine: (1) the importance of biological control factors such as overcrowding, sex ratio, insect predators and parasites, fungi, etc.; and (2) the importance of slash character, bark and phloem thickness, shading, temperature and moisture, and host preferences between slash and living trees. During the course of these studies much was learned also about the habits and cycle of Ips confusus as related to the Miami locality at elevations between 4,000 and 5,000 feet. The information obtained is presented here as a record of progress during the 1946 season.

MATERIALS AND FACILITIES FOR STUDY

Most of the basic field data and materials for experiments were obtained in the Hugh Ryan logging slash area located 2 miles south of the Miami base. Fresh logging slash material laid down continuously from May through September was attacked heavily by Ips confusus and there was provided a continuous supply of broods of any given age desired. Field records on brood abundance and development, and on biological and ecological factors were taken from five separate broods established at different intervals during this period. Brief descriptions of the five slash areas from which these records were taken are as follows:

Area No.	Elevation	Trees Felled	Events and Dates Slash Attacked	 Brood Matured	 Brood Emerged
1	4,300	Fall, 1945	Apr.-May, 1946	6/15/46	6/30-7/31/46
2	3,700	May, 1946	June, 1946	7/8-15/46	7/20-8/10/46
3	4,400	June, 1946	6/25-7/15/46	7/28/46	8/13-
4	3,600	July, 1946	7/11/46	7/28/46	8/20-
5	3,700	Aug. 1-15,1946	8/14-9/3/46	9/20/46	- - -

3/ Struble, G.R. 1946. Slash Breeding by Ips in Relation to Subsequent Attacks on Living Ponderosa Pine. Progress Report of Sierra Studies - 1945

A sixth slash area in which trees were felled between September 1 and 15 was not yet attacked by October 26, 1946. The relatively steep topography of the Hugh Ryan area, broken by ravines and ridges provided a variety of exposures and temperature conditions within short distances from each other where differences in brood produced under separate conditions could be studied. (Photo 1)

Additional field data were obtained from infested slash material from a pole clearing near Miami Lodge, and from logging slash in the vicinity of Footman Ridge and Jerseydale. In all areas Ips confusus was found as the predominant species. Ips sp. (near oregoni) was found only in Area #1, in slash which had been laid down during the fall, 1945.

Laboratory and rearing facilities for studying the habits of Ips confusus and the influence of sex ratio on brood production were provided at the Miami field base. Rearing cages with muslin sidewalls were highly satisfactory in inducing attacks on short log lengths. Sealed cardboard cartons containing infested slash with emergence exits into shell vials proved best among three types of emergence cages used. Refrigeration facilities at the Miami base were used to store Ips adults for future use in the sex ratio rearing tests. (Photo 2)

SEASONAL HISTORY AND HABITS

Number of Generations

During the active developmental period from May through August, 1946 in the Miami area breeding was continuous in available fresh slash material. The peak attack period occurred during the latter part of June and through July. From August 15, until September 15 there was a gradual slackening in number of attacks until by the end of that period there were no new attacks observed in fresh slash. This continuous breeding throughout the summer months resulted in a constant supply of all developmental stages and overlapping generations.

At least three generations were produced during spring and summer in the Miami area in 1946, as indicated by information from dated attacks, field notes, and emergence records from the five separate slash areas, four emergence cages, and one complete rearing record from attacks through emergence. The total period from first attacks to last emergence among these ten recorded cases is tabulated below.

Sample No.	First Attack Date, 1946	Days to First Emergence	Days to Last Emergence
1	May 2	59	88
2	June 1	49	70
3	(June 5) 1/	47	76
4	(June 5)	55	76
5	July 5	46	90
6	(July 5)	43	90
7	July 5	39	77
8	(July 11)	42	84
9	July 11	40	-- 2/
10	Aug. 14	62	-- 3/

1/ Parentheses indicate approximate date.
2/ Emergence approximately 90% complete after 101 days on October 20.
3/ Emergence approximately 50% complete on October 26, remaining adults to overwinter.

On the basis of these data it may be assumed that under normal conditions of temperature at this elevation there are four generations of Ips confusus per year, with the dates of each generation as follows:

Date	Generation
April 15 to June 15	I
June 15 to Aug. 5	II
Aug. 5 to Sept. 30	III
Sept. 30 to Overwinter	IV

Positive proof of a strong fourth (overwintering) generation passing the winter in varying stages of larvae, pupae, and new adults has not been established definitely. By late October, 1946 there were still no attacks in fresh slash laid down in the fall, hence the probability of a sizeable immature brood overwintering in slash was small. 4/ Very few pole-sized trees and saplings had faded by this time, indicating some doubt as to the probability of a large overwintering immature brood in standing trees. Rather it is apparent that the great bulk of overwintering populations are adults of different ages.

In the Jerseydale logging slash area, 20 miles west of Miami, late summer and early fall attacks in living merchantable sized trees, and poles were numerous, resulting in heavy broods which matured and emerged partially before mid-October. There was no evidence of later fading trees toward the end of October, hence it is not known in that area also the size of overwintering populations of immature brood stages.

4/ A check of overwintering broods at Yosemite, Miami, and Jerseydale in March, 1947 revealed that the main body of populations during the winter 1946-47 were in the adult stage from callow to black, but predominantly black. Large larvae and pupae were extremely scarce. Slash created in September, 1946 remained unattacked during fall and winter.

Abundance of Broods

The amount of brood produced per inch of egg gallery, or per unit of bark area, as determined from samples taken under average good breeding conditions in slash throughout the summer indicated: (1) relatively unfavorable breeding conditions in overwintered slash attacked during the latter part of April and in May; and (2) very favorable breeding conditions in fresh slash laid down during May, June, and July. In Table 1 a comparison in amount of total brood, brood per square foot, and brood per inch of gallery between three slash areas and laboratory rearing experiments is presented. All counts were made at the time the brood had reached advanced developmental stages, namely last instar larvae, pupae, and callow adults.

Table 1. Number of Ips confusus brood in different seasonal samples of infested slash.

Age of Slash	No. of Samples	Attack Dates 1946	Total Bark Area Sampled - Sq. Ft.	Total Inches of Egg Gallery	Amount of Brood Produced Total	Per Sq.Ft.	Per Inch of Egg Gallery
Fall, 1945	8	May, 1946	13.79	747	590	42.8	.79
May, 1946	8	June, 1946	8.26	444	1422	172.0	3.20
June, 1946	6	June-July	7.55	507	1544	204.5	3.04
Fresh		Induced rearing 1/	27.00	1576	4752	176.0	3.01

1/ Periodically induced attacks in fresh slash under controlled rearing conditions from July 12 to August 22, 1946.

The large size of broods shown here during the summer in slash material is indicative of ideal breeding conditions. For the present at least it is interpreted as the maximum amount produced under exceptionally favorable conditions. This high population level was fairly uniform in distribution through slash material in different areas investigated. Under conditions allowing general maximum population development it appears probable that the resultant sudden increase over a normal population level might well be responsible for an unusual aggressive attack on living trees.

Adult Emergence and Attack Period

Emergence, flight, and attacks by Ips confusus adults occurred continuously in the Miami area throughout the season in slash material. Emergence data from rearing records established between June 30 and October 3 showed constant emergence of adults from broods established at different intervals during the entire period. The heaviest emergence occurred between July 15 and August 20. Corresponding records of attacks established in slash between May 1 and September 19 showed that the heaviest attack occurred during the time when adults were most numerous and when adult emergence was at a peak period.

Adult feeding Habits

During the period between transformation to adults from the pupal stage and emergence of the full grown adult there is considerable mining under the bark by the adults. This results often in the complete pulverization of the phloem between the original egg galleries. This mining has long been interpreted as a feeding habit, and this is probably correct. Following emergence and attack in fresh slash or in living trees the feeding by adults is presumed to continue along with the construction of egg galleries.

During the course of the 1946 observations in the Miami area an additional feeding by Ips confusus adults in living trees was observed for the first time during the latter part of August. 5/ In several cases examined, involving 12 saplings and the tops of six top-killed merchantable sized trees, the feeding of adults appeared to be primary and reproduction secondary. For example, in one 3-inch sapling, 5 feet high, there were 627 adults in 7 feet of infested length (2.45 square feet of area) from the root collar upward. Most of these adults had attacked the sapling to feed as evidenced by numerous short mines radiating in all directions (See Photo 3). Others constructed normal egg galleries and developed a moderate brood which had developed to last instar larvae.

In another outstanding example in the top-killed portion of a merchantable sized (24 inches d.b.h. x 7 logs) fast-growing tree, a one-square-foot sample of infested length yielded 173 parent adults, 171 larvae, 145 pupae, 13 new adults. Here the total brood amounted to 329 and total population to 502 individuals of Ips confusus. Numerous feeding channels in addition to the brood galleries presented proof of the feeding by many adults not actually involved in reproduction.

Sex ratio of adults

Sex determinations were made on 1,983 adults divided as follows: spring brood - 237; early summer broods - 1,144; mid-summer broods - 273; attacking adults - 51; feeding adults - 288. Adults from all broods had emerged normally and were collected in rearing cages. All determinations were made with the aid of a binocular microscope, with distinguishing characters based on differences in the size of elytral declivity spines, especially the median spine. (The percentage error in determinations as revealed by rearing tests of males and females separately amounted to approximately 15 percent.)

5/ A very similar feeding habit by Ips lecontei, near Prescott, Arizona, was noted by Miller in 1928 under Hopk note #17849. Miller stated: "These (large groups) of adults appear to be feeding but they are not extending egg galleries and are apparently only harboring in this tree". In a published note by Keen (Jour. Econ. Ent.: Feb. 1933) - the attack and mining of phloem in living trees by several species of Ips and Pityophthorus is discussed as a hibernating habit. In the light of what is now known about Ips confusus it is probable that some of the insects attacked these trees to feed rather than to hibernate.

These determinations revealed: (1) that there is apparently no significant difference in sex ratio between different seasonal broods; (2) that the sex ratio of emerging adults is one male to 1.3 females; (3) that the sex ratio of feeding adults is the same as emerging adults; (4) that the sex ratio of attacking adults is one male to 2.5 or 3 females on the basis of limited data.

INFLUENCE OF BIOLOGICAL FACTORS OF CONTROL

Predacious and parasitic Insects.

Several species of predators and parasites were found beneath the bark infested by Ips confusus and were also collected from rearing cages. Two species of predators were outstanding in number and frequency of occurrence. These were Medetera aldrichii (Wh.), Diptera, Dolichopodidae, and Thanasimus lecontei Lec., Coleoptera, Cleridae. Predators generally were more numerous and frequent than parasites. The parasites most often found were tentatively identified as Coeloides dendroctoni Cush., Hymenoptera, Braconidae, and Pachyceras ecoptogastri Ratz., Hymenoptera, Pteromalidae. The number and frequency of the various predators and parasites among 30 samples of infested slash are given in Table 2.

Table 2. Predators and Parasites Associated With Ips Broods

Order	Family	Genus and Species	Total Number	%	Occurrence (cases)	% Occurrence
Diptera	Dolichopodidae	Medetera aldrichii	90	21	12	40
Coleoptera	Cleridae	Thanasimus lecontei	59	14	16	53
	Colydiidae	Aulonium longum	77	18	11	37
	Othniidae	Othnius lububris	58	14	10	33
Hymenoptera		(All species) 1/	33	8	9	30
Coleoptera	Ostomatidae	Temnochila virescens	20	5	13	43
	Staphylinidae	Phloeonumus sp.	22	5	6	20
Diptera	Lonchaeidae	Lonchaea sp.	17	5	5	17
Coleoptera	Colydiidae	Lasconotus laqueatus	10	3	5	17
	Histeridae	Platysoma punctigerum	10	3	4	13
		Plegaderus nitidus	6	1	5	17
Hemiptera	Anthocoridae	(all species) 2/	12	3	3	10
Coleoptera	Cleridae	Enoclerus sphegeus	6	1	1	3
	Staphylinidae	Nudobius sp.	1	0.0	1	3
			421			

1/ Tentative identifications of other parasites found are: Coeloides brunneri Vier. and Atanycolus anocomidis Cush., Hymenoptera, Braconidae; Cecidostiba Burkei Cwfd. and Pachyceras ecoptogastri Ratz., Hymenoptera, Pteromalidae; and Copidosoma sp., Hymenoptera, Encyrtidae.

2/ There appeared to be two or three species of anthocorids, but these have not been identified.

Among these insects Medeteras aldrichii, Thanasimus lecontei, Aulonium longum, and Temnochila virescens occurred often enough and in numbers sufficient to be judged as controlling agents. This does not mean, however, that others, particularly the hymenopterous parasites may not be judged as important in other years because of an increase in their number.

No accurate measure of the amount of control exerted by any single species or all of the species of predators and parasites combined was possible in these studies under field conditions. The only measure used was through comparison between the total number of parasites and predators in measured areas of bark and the total number of Ips brood produced (mature brood only), among different seasonal samples. A summarization of these data in Table 3 includes 29 samples representing 5 different broods in bark areas totalling 39.24 square feet.

Table 3. Number of Living and Dead Ips confusus and Total Enemy Population per Square Foot Among 1946 Broods.

Brood No.	Date Established 1946	Area of Samples Sq. Ft.	Number of Ips and Enemies per Square Foot		
			Ips confusus		Enemies
			Living	Dead	
1	Apr.-May	13.79	142.7	3.4	9.7
2	May-June	8.26	172.0	.8	9.8
3	June	7.55	204.0	2.3	9.1
4	June	6.60	100.0	5.7	12.9
5	July	3.04	79.0	16.7	19.4

These data do not indicate a measure of control consistent with an increase or decrease in Ips populations. Fluctuations in the Ips populations occurred despite a fairly constant number of insect enemies. For example, the number of enemies per unit of infested bark area among spring broods remained at the same level among May and June broods, while the Ips broods produced during May and June rose to nearly 5 times the spring broods. Ips broods produced in late June and July dropped to less than half that of the early summer broods, while the enemy populations rose appreciably. The cause of this drop, however, is not attributed to the increase in enemies. It is more logically attributed to some other biological or ecological factor, and also to an error resulting from too few samples of July broods.

The low level of Ips populations of the April-May broods likewise is attributed not to the presence of insect enemies, but to conditions of the slash. This slash was laid down in the fall, and after a winter of exposure to the elements, fungi, etc., would probably lose much of the nutritional elements as well as conditions favorable to healthy brood development.

Sex Ratio of Ips confusus

The possibility that inequalities in distribution of sexes in certain broods would subsequently influence the number of progeny was investigated. This was done through laboratory determinations on sexes of emerging adults from different seasonal broods and through induced controlled rearings with a control on the sex ratio of attacking adults. As stated previously the sex ratio among the different Ips broods produced in 1946 on the basis of data obtained remained nearly constant or one male to 1.3 females.

In the controlled rearing tests three replications were made with sexes distributed in ratios of 1-1, 1-3, and 1-6 (males to females). Attacks were induced inside small cages with muslin sidewalls on freshly cut short logs each containing 3 square feet of bark area. As a rule, the adults were admitted to attack late in the afternoon or evening to minimize the effects that light might have on immediate attacks. The bark was removed from each log for detailed examinations after 30 days, when broods had reached maturity. The results as shown in Table 4 revealed no significant differences in populations between the different tests regardless of sex ratio differences.

Table 4. Number of Attacks, Length of Egg Galleries, and Amount of Brood Produced.

Sex Ratio	Bark Area Sq.Ft.	Attacks	Egg Gallery Length inches	Total Brood	Brood/Sq.Ft.
1-1	9	86	526	1,778	197
1-3	9	66	557	1,471	164
1-6	9	70	493	1,503	167

These tests demonstrated that at least in these sex ratios there was no appreciable effect on the number of progeny. This might be considered an expected result inasmuch as the limited amount of data on sex ratio of attacking adults showed a ratio of 1 to 3 as mentioned previously. Even where the ratio was 1 to 6 there were still enough males to fertilize all of the females, resulting in a full progeny complement.

Inasmuch as the sex ratio remained constant at 1 to 1.3 in different broods it is not likely that this ratio will change. Hence, the probable occurrence of a sex ratio of attacking beetles greater than 1 to 6 or even greater than 1 to 3 is remote. Therefore, it appears that the sex ratio factor bears no significance in influencing Ips populations.

Feeding habit of adults.

The feeding by adults in living trees late in the summer as mentioned earlier, instead of reproducing progeny in these trees may be an important factor in the reduction of populations. While this habit has not been investigated in detail, it is quite probable that many of the adults not engaged in establishing broods are lost for this purpose. With 150 to 250 attacking adults per square foot under the bark, and only 24 to 40 needed

for the establishment of normal broods, it is evident that the excess numbers are useless in building progeny in these trees. Then in addition, they compete directly with the broods for food supply and may in many cases reduce the supply below the needs of all the progeny to reach maturity.

It was definitely established that the feeding adults abandoned these green trees about the same time as the parent adults of progeny. This occurred from 4 to 6 weeks after the establishment of attacks in the trees under observation. Whether they re-attack new trees and establish broods is unknown. 6/ The additional flight, however, subjects these adults to greater hazards and subsequent losses in their number than would be expected normally.

This feeding habit is believed to be irregular in occurrence as are the attacks in living reproduction, poles, and tree tops. The factors underlying its occurrence and the general exit of adults from slash to living trees late in the season only in certain years are not understood. This is one of the most interesting and may prove to be one of the most important phases in the habits of Ips confusus which when understood may help to explain the sudden end of aggressive killing after only one season of activity.

Fungi

The data obtained on the relative importance of fungi as an agency of control are insufficient for more than tentative conclusions. Among the 30 study samples taken under field conditions, only 4 to 10 percent, contained enough fungus growth to be assigned as a possible cause of Ips brood reduction. In addition, observations of infested slash material under different exposures and conditions of treatment indicated that fungi and/or bacteria might account for conditions which prevented brood development in 25 percent of the slash material laid down.

It is noteworthy that among all the 1946 observations, no case was found in which the mortality of brood could be attributed to a direct attack by fungi. In all cases where fungi or other plant growth was abundant enough to be cited as a cause of brood mortality, the cause appeared to be the result of inadequate or ruined food supply following rapid fungus growth and contamination of the phloem. The presence of excessive fungus contamination appeared to be associated with excessive moisture conditions, such as in slash laid down in the fall and exposed to winter saturation by snows, and also in fresh large-diameter slash from which limbs were lopped.

6/ An additional observation in March, 1947 in a group of 10 fading saplings near Grouse Creek in Yosemite National Park revealed that these young trees contained groups of mature adults feeding in a manner similar to that observed last summer. These trees which were attacked last fall were found to contain no mature brood or young adults.

These observations do not preclude the possibility that direct attacks are not at times made by some species of fungi. Direct attacks by a bluish-green fungus (possibly penicillium) have been indicated in observations made many times previous to 1946. This fungus did not occur in sufficient quantity during 1946 to be considered as a mortality factor.

INFLUENCE OF HOST CONDITIONS

Character of Slash Attacked.

Fresh slash, normally conducive to attacks by Ips confusus under field conditions may be classified because of its physical characteristics and possibility for control treatment into three distinct types as follows: (1) large logs (butts or cull logs) varying in diameter up to 40 inches, usually having most of the branches lopped or broken off; (2) tops of trees with branches attached (basal diameters often greater than 16 inches and tapering to 4 inches) which are of no value for lumber; (3) large limbs varying in diameter (usually 3 to 8 inches), some cut from the main bole and some remaining attached to the log. These three types of slash were regularly and heavily attacked under the conditions of adequate shading during the summer season, but there were variations in the success of brood development through to maturity in the different types, even though the intensity of attack was similar. In the first type, for example, the number reaching maturity was so small in 1946 as to be disregarded as an important source of increasing populations. The second type, on the other hand, yielded consistent heavy populations through to maturity while the third type yielded variable populations from poor to heavy depending apparently on the amount and rapidity of drying. Thus, it was revealed that the top sections of trees from which the merchantable logs had been bucked were not only the most prevalent type of slash, but also the most ideal from the Ips breeding standpoint, and therefore, most important from the standpoint of control. This appeared to be true regardless of the age or vigor of the trees from which the slash was accumulated under similar conditions of temperature, exposure, or shading.

Reasons for the variations in brood success in these slash types were due evidently to differences principally in moisture content during the period of brood development. In the tops of trees with all limbs attached, for example, the gradual drying of the phloem layer because of active transpiration by the green foliage for a short period was evidently ideal from the brood development standpoint. Too rapid drying in the lopped limbs often resulted in the development of poor broods or the excessively moist conditions in large logs because of lopped limbs resulted in the development of poor broods.

Bark and Phloem Thickness

Studies of these factors and their possible effect on the production of mature Ips broods revealed no significant correlations as shown in

Table 5. Phloem even as thin as 1/16 inch proved to be highly productive of broods, at least in the areas examined, which indicates that the food supply and other factors such as moisture and temperature were adequate for the development of a full brood.

It is unlikely that bark thickness, at least in the range of thicknesses investigated, would have any influence on the brood, except as it may influence evaporation of moisture with some subsequent effect on the development of broods to maturity. Greater thicknesses than those investigated may affect brood production because of the possibility of excessive moisture, especially if the moisture is not drawn off through transpiration.

Table 5. Number of Ips per Square Foot in Different Thicknesses of Phloem and Bark

Thickness Inches	Number of Samples	Bark Area Sq. Ft.	Brood Per Sq. Ft.
	Phloem		
1/16	2	1.48	223
3/32	4	5.82	103.2
1/8	9	11.46	185.5
3/16	3	3.65	105.6
	Bark		
3/16	3	2.52	189.0
1/4	2	3.86	73.5
5/16	1	2.20	160.9
1/2	8	10.16	157.7
5/8	4	3.66	195.5

Degree of Shading

Limited investigations were made of the brood development in relation to three intensities of shading as follows: (1) in open sunlight with shade provided only by the foliage of limbs attached to the slash material; (2) in semishade provided by trees growing in the vicinity of the slash; and (3) in full shade provided by fairly dense growth and foliage of the slash material. Under these conditions it was found that attacks were uniform. Therefore, any differences in the amount of brood produced to maturity would likely result indirectly from the effects of shading. The data as presented by Table 6 which follows, indicate that the amount of shading may be a factor in population production through its effect on temperature and evaporation of moisture.

Table 6. Number of Brood per Unit of Bark Area Under Different Degrees of Shading

Degree of Shading	Number of Samples	Bark Area Sq. Ft.	Brood Per Sq. Ft.
Open	8	8.75	172.9
Semi-shade	9	11.40	154.0
Full shade	5	5.30	66.5

Some significance on the effects of different amounts of shading was indicated. Evidently larger broods were produced in slash lying out in the open where shade was provided only by the foliage of the slash itself than under more shaded conditions, and under fully shaded conditions the broods were smallest. Reasons for this might be explained on the basis of moisture conditions, i.e., out in the open the moisture in slash is apt to dry out more in line with conditions required for satisfactory brood development, whereas under shaded conditions an excess of moisture might stimulate the growth of fungi which are detrimental to brood development.

Moisture and temperature.

The limited investigations of host conditions as they may affect populations tend to emphasize the importance of temperature and moisture. Relative measurements of these two factors alone were not made during 1946. However, observations on comparative dryness or wetness under different temperatures permitting attack and relating the condition with abundance of mature broods strongly indicated that moisture is a key factor in population increases or decreases. If so, weather, particularly atmospheric humidity, may contribute materially to the development of sudden outbreaks by stimulating or preventing loss of moisture in slash material attacked by Ips.

The moisture required for an adequate environment of developing Ips broods is apparently quite exacting, deviations from which are evidently detrimental if deficient or excessive. However, before it is possible to draw conclusions on this point much data must be taken, especially during the period of development of Ips broods from attacks through maturity of broods.

Studies by Beal 1/ in 1931 indicated that Ips oregoni were not impaired in their development through a wide range in phloem moistures. Beal states that, "On slash and logs of all sizes, from 1 inch diameter to 3 feet, Ips oregoni have produced heavy broods under moisture conditions from 50% or less up to 400%." This is in constrast to present indications from observations on Ips confusus which indicated that Ips confusus requires a moisture environment which is similar to that which Beal found to be required by D. brevicomis, namely, that "the most successful brood in logs was that found under the driest conditions" where the logs "dried out from 173 to 88%"phloem moisture. Beal's moisture data through the brood development periods of Ips oregoni and D. brevicomis which consider data only from two logs and one standing tree, however, appear too limited upon which to base general conclusions on the moisture requirements.

Host Preference Between Slash and Living Trees.

The late summer and early fall attacks in living trees, repeatedly observed by entomologists over the years indicated: (1) either that there were

1/ Beal, J.A., 1931: Further Studies on Insects in Logging Operations in Western Yellow Pine.

preferences by certain Ips broods for living trees instead of slash, or (2) that seasonal changes in the living host set up an attraction stronger than the fresh slash. The first point was tested during the 1946 season in an experiment to determine if certain seasonal broods in slash would suddenly prefer the living trees to fresh slash. This experiment was carried on inside a screened cage enclosing three moderately growing ponderosa pine saplings from 6 to 8 feet in height. Infested slash containing callow adults was placed among the saplings and also freshly cut green ponderosa pine slash. Emerging beetles were thus given an equal choice between the fresh slash and living trees for their attacks. The experiment was repeated three times with different seasonal broods on the following dates: Test #1, June 26 to July 22; test #2 July 22 to August 15; test #3, August 15 to Sept. 18.

The results of these tests are described briefly. In tests 1 and 2 a few unsuccessful attacks were made on two of the saplings, while the slash in both tests was heavily attacked. In test 3 two of the saplings were attacked heavily and killed, while the slash was moderately attacked. The third sapling remained free from attack.

Concurrent with attacks inside the cage, an attraction attributed to the experiment itself evidently caused Ips in flight to be drawn into the vicinity of the cage, and presumably because they could not enter, they attacked saplings surrounding the cage. The first sapling died as a result of attacks on July 22; eight more saplings were attacked and killed during the week ending August 13; one more sapling was killed on August 20, one more on August 28, and another on September 18. Thus 12 saplings in the immediate vicinity of this cage were attacked and killed, most of them during August. (Photo 4)

The evidence from the three tests and also the attacks made on living trees outside the cage indicated that attractiveness of the living trees increased with the advance of seasonal conditions rather than any disposition on the part of a particular brood to suddenly attack living trees. This appears to be a response to increasing attractiveness which may develop following the active growing period of the host trees themselves because of certain physiological changes taking place.

DISCUSSION AND CONCLUSIONS

These 1946 studies of Ips populations in slash in the Miami area are of necessity preliminary and exploratory. For one thing an understanding of this problem so that it may be controlled properly requires an indefinite period of study because of many complex variables. Before it will be possible to draw sound conclusions it will be necessary to carry forward intensive studies for a period which includes the high, the low, and the intermediate stages or phases of fluctuating populations, and their relation to host environment. This may require a minimum of five years. What

appears to be a true picture of the biological cycle of Ips and its relation to natural controlling factors in a given locality this year may be altogether different next year. What happens in one locality in a given year may be altogether different in another locality during the same year.

Reasons for the differences between years in the same locality or between different localities during the same year can be attributed to any one of several factors or combinations. The 1946 studies in the Miami area, immediately applicable only to that area, indicated several factors which seemed important in explanation of the development for that year. These studies were undertaken at a very opportune time when adult populations had apparently approached or reached a peak in numbers which resulted in an aggressive attack in living trees. This was in contrast to the events of the previous year in which, although attacks and brood in slash were numerous, there was no aggressive killing of living trees. What will happen in 1947 is to be determined.

Outstanding among factors which may contribute to sudden fluctuations in adult populations as indicated by the 1946 studies were: (1) the feeding habit by adults in living trees in lieu of reproducing, and (2) the moisture environment of developing Ips broods from attack to maturity. Their seemingly immediate significance indicates that these two factors should be investigated thoroughly in future studies. As to the feeding habit, it is doubtful if much may be learned short of several years of investigation because of the apparent irregularity of this habit. Studies on the moisture factor, however, can be started at any time and may within a relatively short period yield significant results.

Two other factors studied in 1946 which did not appear significant, but which may be highly important in other years are: (1) biological control by insect enemies; and (2) biological control by fungi. The facts learned on biological control by insects in 1946 indicated that they were relatively unimportant either as a group including all species or as single species among those that were most prevalent. But what happened among the 1946 broods does not mean that certain species may at times become numerous enough to be important in suddenly reducing Ips populations. This might well be true of certain of the predators such as Medetera aldrichii or Thanasimus lecontei, but is not so likely among the parasites.

One fact regarding the insects involved in biological control in the 1946 observations was that almost without exception nearly all species of the predators in the larval stage were in very early stages of development at the time of examinations of mature Ips broods. This would indicate either that there was a scarcity of adult predators at the time Ips attacks were made, or that the predators were much slower in development than Ips. While both facts may be partly true, there is reason to believe, on the basis of previous investigations on predators 8/, that in other years more advanced stages of predator larvae will be found which may result in appreciably more control.

8/ Struble, G. R. 1942. Biology of Two Native Coleopterous Predators of the Mountain Pine Beetle in Sugar Pine. Pan Pacific Entomologist: XVIII, No. 3.

The same thing insofar as biological control by insects in concerned can be said of certain fungus organisms, especially of the blue-green fungi mentioned previously, that may directly attack the developing Ips broods. Other fungus organisms on the other hand, may affect the developing Ips broods indirectly by using up their food supply. Their presence may be largely influenced by the amount of moisture which can be controlled in slash.

SUMMARY

Detailed exploratory studies of the biological and ecological factors underlying the epidemiology of Ips confusus as related to slash breeding and subsequent aggressive infestations in living trees were undertaken at the Miami Field Base from June 15 to September 15, 1946. Most of the information was obtained from logging slash in the Hugh Ryan logging area which is 2 miles south of the Miami Station. Continuous supplies of fresh slash throughout the summer provided an abundance of infested material for study. Most of the records related to five separate slash areas established from three to four weeks apart.

The most important facts learned from this study are listed.

1. Ten records from different seasonal broods from attacks through emergence indicated that there are four generations of Ips confusus each year in the Miami area.

2. The emergence, flight, and attack periods are continuous throughout the late spring and summer with a peak period between July 15 and August 20.

3. Favorable breeding conditions in slash during 1946 resulted in the development of consistent large-sized broods, approaching an average number at maturity of approximately 175 per square foot or three individuals per inch of egg gallery.

4. The large number of adults emerging from slash during August resulted in aggressive attacks on living reproduction, poles, and the tops of merchantable sized trees.

5. In living trees concentrations of attacking adults varying in number from 150 to 250 per square foot revealed a feeding habit in lieu of reproduction not heretofore reported for this species, which is a competitive factor with newly established progeny and may have an important bearing on sudden reductions in a high population level.

6. Sex ratio determinations of 1,983 adults revealed a ratio of emerging adults of 1 male to 1.3 females; a ratio of attacking adults of 1 male to 3 females.

7. Controlled rearing tests to determine the importance of sex ratio on brood production revealed that under normal conditions in the field this factor bears no significance in influencing populations.

8. Studies of insect enemies as they may influence Ips populations revealed that they were of no relative importance in 1946, either as a group or by single species, but this does not necessarily mean that they may not be important in other years.

9. Limited data on fungi as a possible agency of biological control of Ips indicated that it is important under excessively moist conditions where its growth contaminates and ruins the food supply of Ips confusus. Direct attacks by fungi, previously suspected to be of possible importance , were not found in the 1946 studies.

10. Studies of possible host preference between slash and living trees by different seasonal Ips broods revealed a preference for living trees during August and September, but this is believed to be a response to physiological changes in the host following seasonal growth which may render the host more attractive at that time.

11. Studies of ecological factors relating to Ips development in slash indicated that the tops of trees with limbs attached provided the most ideal breeding conditions, because of the gradual drying of phloem induced by the transpiration of green foliage.

12. Excessively moist conditions in logs or tops with lopped limbs resulted in poor broods, even though attacks were heavy.

13. Limbs 6 inches or less in diameter often yielded poor broods because of too rapid drying, especially in mid- or late- summer.

14. Studies of phloem and bark thickness as they may relate to numbers of brood produced revealed that these factors are apparently of no significance.

15. Limited studies of the effects of various degrees of shading revealed that there appears to be a slight influence, but this is believed to be due to the effects of shading on moisture within the slash material.

16. While no studies were made directly on the effects of moisture, the results of studies of other ecological factors all point to moisture as a key factor in the successful production of large Ips populations--that brood success appears to be dependent on a gradual reduction in moisture through the larval development stages, excesses or deficiencies of which may be detrimental.

Photo #1. Looking east across the Hugh Ryan basin toward Speckerman Mountain. The slopes of the middle foreground, consisting principally of ponderosa pine were selectively logged during 1946. An abundance of slash provided ideal breeding conditions for Ips confusus.

Photo #2. Miami Field Base, Bureau of Entomology & Plant Quarantine. Laboratory and rearing facilities for the Ips studies were furnished here.

Photo #3. Feeding habit of attacking Ips adults. Bark removed from base of 3-inch sapling to expose a maze of feeding galleries bored by hungry adults during August, 1946.

Photo #4. Screen cage used in testing host preference between fresh slash and living saplings. The cage enclosed infested slash, fresh slash, and three living ponderosa pine saplings. During August the experiment attracted Ips adults in flight which attacked and killed twelve of the saplings in the immediate vicinity of the cage.